Rates of Food Passage in the Digestive Tract of Young Desert Tortoises: Effects of Body Size and Diet Quality

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NOTES and FIELD REPORTS

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Abstract. – Diet quality and body size affected passage time of 2 diets (higher and lower in fiber) in hatchling and juvenile desert tortoises (*Gopherus agassizii*). Mean retention time of the liquid fraction of each diet was significantly shorter than that of the solid fraction, and hatchlings had shorter passage times than juveniles. Habitat disturbances that limit access of hatchlings to diets lower in fiber may negatively impact the physiological and behavioral ecology of young desert tortoises.

Desert tortoises (*Gopherus agassizii*) eat diets composed primarily of annual grasses and forbs, and the digestibility of those diets can vary within and among years (Nagy and Medica 1986; MacArthur and Sanderson 1992; Esque 1994). More easily digestible diets have lower amounts of plant structural materials, including hemicellulose, cellulose, and lignin (i.e., cell wall or "fiber"), and higher concentrations of nitrogen (principally protein and other cell solubles). Herbivorous reptiles, including members of the turtle family Testudinidae and the lizard family Iguanidae, can digest fiber as well as, or better than, herbivorous endotherms (Throckmorton 1973; Bjorndal 1979, 1987, 1989; Hamilton and Coe 1982; Zimmerman and Tracy 1989; Bjorndal and Bolten 1990; van Marken Lichtenbelt 1992; Meienberger et al. 1993). Digestive efficiencies of fiber in these studies of herbivorous reptiles ranged from 37% to 86%, whereas values in mammalian herbivores range from 30% to 65% in nonruminants and from 30% to 75% in ruminants (Van

Soest 1982), depending primarily on diet quality within each group.

Digestion can be more efficient if food is ingested in smaller pieces, but reptiles do not masticate their food (Throckmorton 1976). Nevertheless, younger reptiles typically ingest smaller bites than do adult reptiles (Troyer 1984; Bjorndal et al. 1990), which should enhance digestion. Digestive efficiency also can be enhanced by increasing the time for fermentation in the hindgut. Digestibility of the refractory portions of an herbivorous diet typically increases as retention time increases (Sibly 1981; Allen and Mertens 1988). Retention time, in turn, is affected by body size, rate of food intake, and diet quality (e.g., Meienberger et al. 1993).

Young and growing desert tortoises face resource challenges in their harsh environments (Nagy et al. 1997). Because small tortoises have higher mass-specific metabolic rates (Nagy et al. 1997) and have higher rates of water loss (Wilson et al. 2001), understanding the capabilities of young desert tortoises to process food is important to understanding the physiological ecology and conservation biology of desert tortoises. The objective of our study was to quantify the rates of passage of digesta in young desert tortoises in relation to body size and diet quality.

Methods. — Experimental tortoises were selected from a captive population maintained at Colorado State University (Fort Collins, CO). Tortoises were divided into 2 age (size) classes: hatchling tortoises were less than 1 year old and were 33–77 g in body mass, and juvenile tortoises were 1 to 2 years old and weighed 165–315 g. During the experiment, tortoises were weighed at least once weekly to ensure that they generally gained body mass. Two tortoises that lost considerable body mass (approximately 15%), were removed from the study.

Animals were maintained individually in $25 \times 20 \times 8$–cm plastic cages for the duration of the study. Cage bottoms were fitted with a platform of 1.4-cm mesh wire screen, through which feces passed so they would remain undisturbed by coprophagy or by trampling by tortoises until fecal samples were collected that day. The experiment was conducted in an environmental chamber at 30°C, a temperature at which tortoises were previously determined to perform well, and which was within the eccritic range of field body temperatures of desert tortoises (Zimmerman et al. 1994). Photoperiod was 14 hours light:10 hours dark. Water was available ad libitum.

We used a diet of uniform particle size and water content to control for these variables in 2 dietary formulations differing principally in fiber content. Experimental diets consisted of mixtures of guinea pig chow (Purina #5025) and chick-starter chow (Purina #5035). The low-fiber diet was composed of 50% guinea pig chow and 50% chick-starter chow, and the high-fiber diet was a

Table 1. Partial nutrient composition of low fiber (50:50) and high fiber (90:10) diets.[a]

		Detergent Fiber	
Chow	Protein	NDF[b]	ADF[c]
GP - unwashed	23	37	18
GP - washed[d]	17	69	41
CS	33	26	2
Unwashed Mixtures (Unlabeled)			
50% GP/50% CS	28	32	11
90% GP/10% CS	24	36	16
Washed Mixtures (Labeled)			
50% GP /50% CS	26	47	21
90% GP /10% CS	19	65	37

[a] Values are percentages of the diet. GP = guinea pig; CS = chick starter, NDF = neutral detergent fiber; ADF = acid detergent fiber.
[b] NDF is a measure of hemicellulose, cellulose, and lignin ("cell walls" or "dietary fiber" with soluble components removed). NDF content was within the range for foods comprising the diet of desert tortoises in the Mojave desert (Marlow 1979).
[c] ADF is a measure of cellulose and lignin (i.e., NDF minus hemicellulose).
[d] Washed diets included GP chow from which cell solubles were removed, leaving the fiber fraction.

90%:10% mixture of guinea pig and chick starter chows, respectively (Table 1).

To prepare a marked diet (to be fed at one time prior to fecal collection), guinea pig chow was treated with detergent to remove the soluble material that might interfere with the binding of the marker. "Washed" guinea pig chow was made by placing this chow in a cloth bag (cotton pillow case) and washing it in a household washing machine using hot water and detergent (Ultra Tide Unscented, Procter and Gamble, Cincinnati, OH). The washed chow was then rinsed thoroughly with hot water to remove cell solubles and detergent residues. We ran the washed chow through several rinse cycles to eliminate traces of detergent. The type of detergent used was probably inconsequential but it was important to remove all traces of soap residues from the washed chow to avoid the possibility of digestive disturbance. Following several rinse cycles, we took the absence of foaming as an indication that detergent had been completely removed from the washed material. Washed chow was only used for the labeled diet (fed on 1 day); untreated chow mixtures (Table 1) were used for all other feedings.

Marked experimental chows were labeled with ytterbium (Yb) and cobalt (Co). We labeled the more refractory fiber fraction of food with Yb by the method of Teeter et al. (1984), and we labeled the liquid fraction with Co-EDTA after Uden et al. (1980).

Animals were acclimated either to the high- or the low-fiber food. Then, a single dose of labeled food was given on one day, after which tortoises continued to be fed daily and feces collected for approximately 1 month. For marked and unmarked food, tortoises were allowed to feed freely on a measured amount of food each day, and the orts (remaining uneaten bits of food) were collected daily to determine intake.

For Experiment 1, we fed 12 juvenile tortoises the low-fiber diet ad libitum from 27 March to 2 June. Each day during this period, we fed the animals and collected feces from each cage. On 2 June the tortoises were fed a single dose of food labeled with Yb and Co. Each day thereafter, we continued feeding the unmarked diet while collecting feces produced by each tortoise. Feces were dried in a forced-air oven for 2 days at 60°C and then weighed and stored until analysis.

For Experiment 2, one group of 6 individuals from Experiment 1 was fed the high-fiber diet on 3 July, and the other group of 6 remained on the low-fiber diet. Body mass was matched between the groups by assigning animals of similar size to each group. On 19 July, following an acclimation period of more than 2 weeks, each tortoise received a dose of labeled food as in Experiment 1. Subsequently, animals were fed daily, and feces were collected daily and treated as in Experiment 1.

For Experiment 3, we began feeding 6 hatchling tortoises the low-fiber diet on 26 June. On 3 July, we divided the animals into 2 groups of 3 individuals each; one group continued to receive the low-fiber diet, and the other received the high-fiber diet. On 19 July, we gave each animal a dose of Yb- and Co-labeled food. Animals were fed daily, and feces were collected daily and treated as in Experiment 1.

To prepare dried fecal samples for spectrophotometric analysis, we ground them through a Wiley mill to pass through a 20-mesh screen. We mixed 0.25 g of sample with 0.5 g concentrated sulfuric acid and 1.0 ml of a 50:50 (by volume) mixture of concentrated sulfuric and nitric acids and heated in a block digester at 75°C for 2 hours. After heating, we added 18.5 ml of a 3.8 g/L solution of potassium chloride.

The concentrations of Yb and Co in the digested fecal samples were determined via atomic absorption spectrophotometry. This analysis was conducted at the Colorado Division of Wildlife Laboratory in Fort Collins, Colorado, using an Instrumentation Laboratories Video 22 atomic absorption spectrophotometer with a nitrous oxide flame. Ytterbium was analyzed at a wavelength of 398.8 nm and a bandpass of 0.5 nm. Cobalt was analyzed at a wavelength of 240.7 nm and a bandpass of 0.3 nm.

To calculate the mean time that each marker remained in the gut of each tortoise, we plotted the cumulative amount of marker appearing in the feces as a function of the number of days after dosing. The mean time was taken as the number of days after dosing at which 50% of the marker had been recovered (Van Soest 1982).

Mean times for juvenile tortoises were analyzed in a 5-way analysis of variance using the following independent variables: individual tortoise, experimental group, marker, diet, and marker-by-diet interaction. Mean times for hatchlings vs. juveniles were analyzed in a 4-way analysis of variance using age class, marker, diet, and marker-by-diet interaction as independent variables.
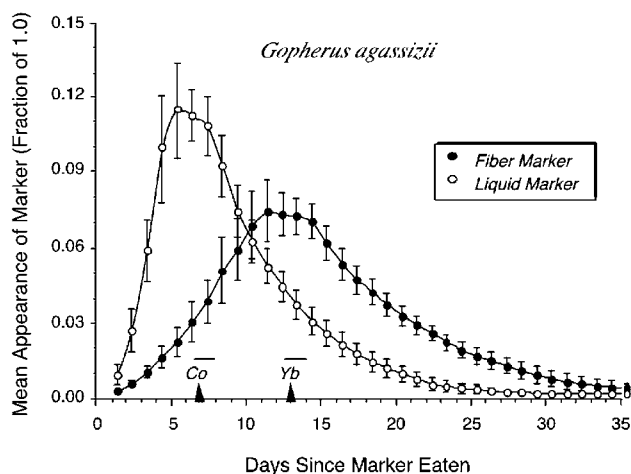
Figure 1. Fractional appearance of ytterbium (Yb) and cobalt (Co) markers in feces as functions of time since dosing the animals. These values are for juveniles fed the high-fiber diet. Each data point is a mean of measured or interpolated levels of marker normalized to 100% of the marker that reappeared in feces. Actual measurements were made every 2 to 4 days, and points from days between measurements were calculated by simple interpolation. Error bars are ± 1 standard error. Mean passage times (50% appearance) for Co and Yb are indicated on the x-axis.

Results. — We recovered nearly 100% of each marker before experiments were terminated. Appearance of Co and Yb in the feces followed different curves for the liquid and fiber fractions, respectively (Fig. 1). A larger percentage of the Co marker appeared at an earlier time during the experiment than did the Yb marker. In the 5-way analysis of variance on mean times for juvenile tortoises, all tested variables statistically explained variance in the data (Table 2). Moreover, we detected a significant interaction between marker and diet quality in juveniles (Fig. 2). This interaction indicates that although the marker of the liquid phase (Co) passed along the gut more rapidly than did the marker of fiber (Yb) of both diets, the liquid-phase marker passed along the gut significantly faster when the animals ate low-quality food (Table 2, Fig. 2).

In the 4-way analysis of variance of mean times for both hatchling and juvenile tortoises (Table 3), the marker-by-diet interaction was significant, and the appearance of markers (Yb vs. Co) was significantly different, indicating that Co passed through the gut more rapidly (7 days, averaged overall) than did Yb (11 days, averaged overall). The size of tortoises influenced passage times, with food taking several days longer to pass through the juveniles than was the case with hatchlings (Table 4).

Discussion. — Passage times in this study were comparable to those of previous studies of digestion in desert tortoises. Transit times of desert tortoises did not differ between juveniles (24 days) and adults (23 days) eating a dry grass (*Schismus barbatus*), but were shorter in juveniles (15 days) compared to adults (20 days) eating a succulent forb (*Erodium cicutarium*) (Meienberger et al. 1993). Mean retention time of desert tortoises on an

Table 2. Five-way analysis of variance on mean passage times in juvenile tortoises.[a]

Source	df	Mean square	F value	p value
Marker (Yb vs. Co)	1	167.703	128.659	0.0001
Diet (high vs. low fiber)	1	12.000	9.206	0.0048
Experiment (first vs. second)	1	12.470	9.567	0.0041
Individual tortoise	11	20.108	15.427	0.0001
Marker * diet	1	26.522	20.348	0.0001
Residual	32	1.303		

[a] This analysis examined components of variance in passage times within juvenile subjects. In the first experiment, all juveniles were fed the high-fiber diet, and in the second experiment, half were fed the low fiber and half were fed the high-fiber diet.

herbage diet (*Sphaeralcia ambigua*) containing 29.1% neutral detergent fiber (NDF) (similar to our diets) was 9.5 days (Barboza 1995). The dietary marker of this herbage, chromic oxide, mainly flowed with the particulate phase of digesta (Barboza 1995). On a grass diet (*S. barbatus*) containing 64.6% NDF (approximately twice the NDF content of our diets), mean retention time of particles (14.2 days for large particles and 9.6 days for fine particles) exceeded that of fluids (6.8 days) (Barboza 1995), as in our study.

Reptiles generally appear to retain the particulate fraction of their diet for a longer time than the liquid fraction. In a previous study of digesta passage in adult desert tortoises, mean retention times of the particulate fractions exceeded that of the fluid fractions on a diet of the grass *S. barbatus* and on a high-fiber pelleted diet (Barboza 1995). Likewise in adult Galapagos tortoises (*Geochelone nigra*), mean retention time of the liquid
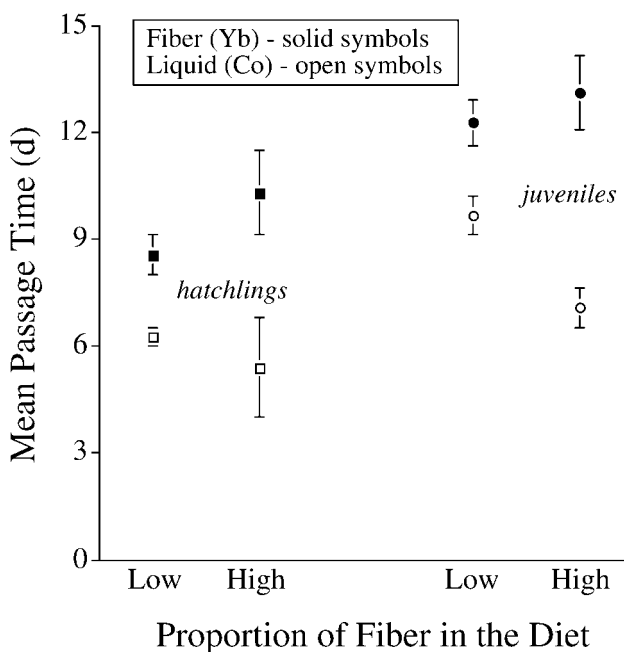

Figure 2. Interaction plot of mean passage time as functions of diet quality and passage marker in juvenile and hatchling desert tortoises. Ytterbium marked the solid fraction of food and cobalt marked the soluble fraction. Error bars are ± 1 standard error.

Table 3. Four-way analysis of variance on mean passage times in hatchling- and juvenile-sized tortoises.[a]

Source	df	Mean square	*F* value	*p* value
Age (hatchling vs. juvenile)	1	57.614	10.711	0.0019
Marker (Yb vs. Co)	1	197.778	36.767	0.0001
Diet (low vs. high fiber)	1	4.391	0.816	0.3705
Marker * diet	1	28.893	5.371	0.0245
Residual	51	5.379		

[a] This analysis examined components of variance in passage times between hatchling and juvenile subjects.

Table 4. The effect of tortoise size on passage time as a function of marker and diet. Ytterbium marked the solid fraction of food and cobalt marked the liquid fraction.

Marker	Diet	Juvenile passage time (d) minus hatchling passage time (d)		
		Mean	Minimum	Maximum
Ytterbium	High fiber	3.7	0.3	7.3
	Low fiber	2.8	−1.4	7.0
Cobalt	High fiber	3.4	0.8	6.2
	Low fiber	1.7	−1.6	5.0

phase of a mixed diet was shorter than for the particle phase (Hatt et al. 2002). Other herbivorous reptiles (*Geochelone carbonaria* and *Iguana iguana*) passed liquid markers more quickly than particles, as did omnivorous *Chrysemys picta belli* and carnivorous *Caiman crocodilus* (Guard 1980). The water-soluble dye of food appeared in feces of the carnivorous lizard, *Sceloporus merriami,* before an insoluble marker did (Beaupre et al. 1993). However, the passage times for solid and aqueous phases of digesta were similar for the carnivorous lizard, *Cnemidophorus sexlineatus* (Hatch and Afik 1999).

Different passage times of the liquid and particulate fractions of digesta (Fig. 1) may enhance the rate of nutrient extraction. Faster passage of the liquid fraction would decrease processing time of the more readily digestible components, and longer retention of the particulate fraction would increase its exposure to cellulolytic endosymbionts to enhance digestive efficiency of the more refractory components of the diet. The interactive effect of shorter retention time of the liquid fraction of the higher fiber diet (Fig. 2) is consistent with the digestive strategy of minimizing processing time and enhancing digestive efficiency of different dietary fractions. In a previous study of the digestive responses of the tortoises *Geochelone carbonaria* and *Geochelone denticulata*, the retention time of the particulate fraction of food varied as a function of diet quality (Bjorndal 1989). The particulate fraction was retained longer for diets containing more cell wall. Passage kinetics of the liquid phase of digesta, however, were not measured in that study. Moreover, the experimental diets of Bjorndal (1989) varied more widely in fiber content (cell wall = 28.6%–58.3% organic matter) compared to our study (NDF = 32% and 36% dry matter). Nonetheless, these findings suggest that tortoises are capable of digestive flexibility in processing a range of food items, and differences in digestion because of age and species remain to be measured.

It is likely that differences in passage rate alone, assuming bulk limitation of food intake, would allow tortoises eating a low-fiber diet to acquire energy and other nutrients much faster than tortoises eating a high-fiber diet. In the wild, food particle size (a controlled variable in this study) will also influence passage time and, consequently,

digestibility of food, as in the herbivorous turtle *Pseudemys nelsoni* (Bjorndal and Bolten 1992) and other herbivores (Bjorndal et al. 1990). Our data suggest that a diet consisting primarily of low-fiber foods could yield much more energy per unit time than could a high-fiber diet. This is particularly important because the range of assimilation efficiencies necessary for sustaining desert tortoises is simultaneously related both to food quality and to the rate at which the forage passes along the gut, thus determining the rate of digestion to provide desert tortoises with nutrients necessary to sustain metabolic expenditure rate.

Compared to adults, young, growing tortoises need higher rates of nutrient assimilation to support their higher mass-specific metabolic rates. Estimated mass-specific field metabolic rates of hatchling (50 g), juvenile (250 g), and adult (2500 g) desert tortoises are 0.102, 0.074, and 0.046 kJ·g^{-1}·d^{-1} (after Nagy et al. 1997). Hatchlings of other herbivorous reptiles have similar digestibilities as adults but attain a higher rate of digestion by selecting higher-quality food (Troyer 1984; Mautz and Nagy 1987; Bjorndal and Bolten 1992) and passing it through the gut more quickly than adults (Troyer 1984; Bjorndal and Bolten 1992; Wikelski et al. 1993). Juvenile desert tortoises forage selectively by consuming plant species and plant parts of higher quality (Oftedal et al. 2002) and pass food through the gut more quickly (this study).

In summary, these findings of differential passage rates suggest that it would be advantageous for young, growing tortoises to have opportunities to specialize on low-fiber diets. Furthermore, any impact on the habitat (e.g., invasion of annual grass weeds) that precludes access to low-fiber foods could constrain assimilation in young desert tortoises. Adults, however, may be better able to tolerate reduced access to higher-quality foods for a longer period of time because of their lower mass-specific metabolism, more voluminous guts compared to subadults, and consequent longer retention times.

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